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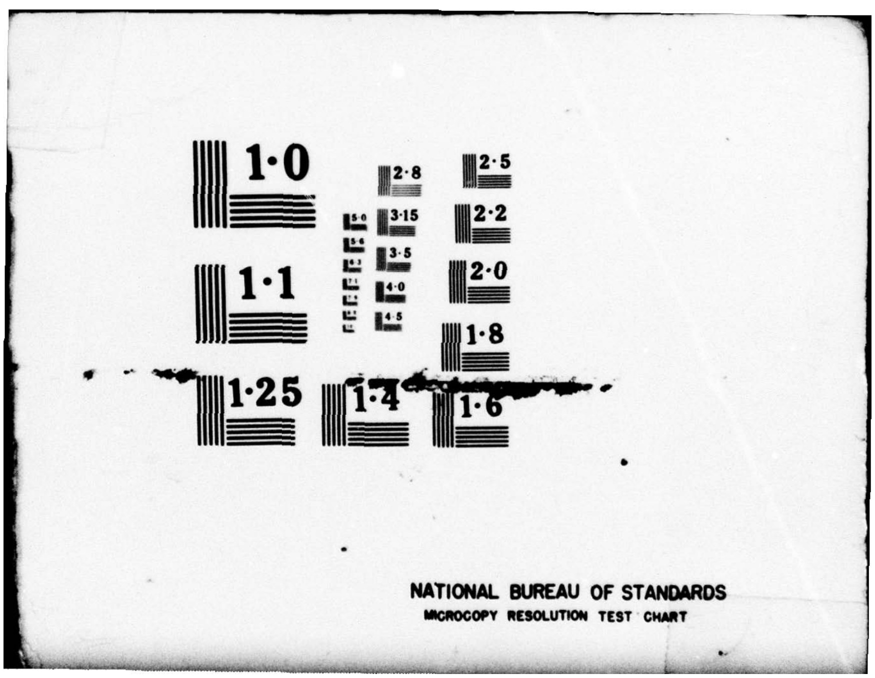
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10 Marc Mangel

14 CNA-PP-224

9 Professional Paper No. 224

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12 53p.

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AGGREGATION, BIFURCATION, AND EXTINCTION IN EXPLOITED ANIMAL POPULATIONS*

Marc Mangel**

March 1978

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INTRODUCTION

In this paper, we consider the following type of harvesting problem. An animal population is divided into two stocks: an "underlying" population and a "surface" population. We assume that there is a natural exchange between the two population levels. The predator or harvestor affects only the "surface" population and does not influence the "underlying" population directly. Such a situation occurs, for example, in the off-shore Eastern Tropical Tuna Fishery (e.g., IATTC, 1975). In this case, tuna associate with porpoise schoools. The fishery harvests only those tuna associated with porpoise. Consequently, the underlying population of tuna is not sampled by the fishery. One may wonder what information measurements on the surface, harvested population provides about the unobservable underlying population. Furthermore, it is interesting and important to know if the standard, linear relationship between harvest and effort is valid in an aggregating population.

Clark and Mangel (1977) studied some of these questions, as they relate to the tuna fishery. They constructed a number of models of the fishery and analyzed the steady state behavior. Some of the models exhibited a bifurcation as harvesting effort increases. Namely, the steady state tuna level, N_∞ , depends on two parameters. The first, α , characterizes natural association and growth rates, while the second, E , characterizes fishing effort. In some of the

models, no bifurcation occurred. In other models, if α is less than a critical value α_c , Clark and Mangel showed that there is a non-trivial steady state $N_\infty(\alpha, E)$ for all E. When $\alpha > \alpha_c$, there exists a non-trivial steady state only if $E < E_b$, some bifurcation value of effort. If $E > E_b$, then $N_\infty = 0$ is the only steady state. Clark and Mangel used a steady state analysis. Here we will study the dynamical equations in more detail, and thus extend the previous analysis.

When the only steady state is the trivial one, the population will approach extinction as time increases. However, for many situations, the time to reach $N(t) = 0$ is not as relevant as the time to reach $N(t) = \delta$, where δ is a given (low) population level. This is true for the following reasons. First, the predator will cease to seek the prey once the prey becomes scarce enough. Second, as $N(t) \to 0$ a model in which N is a continuous variable is no longer valid, since the small value of N demands a discrete model. Third, if the population level becomes very low, the entire dynamics of the species may shift into some other, stable configuration (e.g., a second predator may become important, (see Holling, 1973). We introduce a time $T_\delta(N_o, E)$:

t

$$T_\delta(N_o,E) = \min[t:N(o) = N_o, N(t) \le \delta, N(S)>\delta, \text{for } S< t. E(t)=E] \qquad (1)$$

Then $T\ (N_o,E)$ is the first time that the population goes below the level δ , given that it starts at level N_o and is harvested

with constant effort intensity E. In this paper, we will provide techniques for the approximate calculation of $T_\delta(N_o, E)$.

All predator-prey systems, of course, operate in a random environment. Clark and Mangel did not consider any stochastic effects. When stochastic effects are included, the proper description of the system involves probabilities of certain events. Instead of $T_\delta(N_o, E)$ we must consider the ensemble average

$$\bar{T}_\delta(N_o, E) = \langle T_\delta(N_o, E)\rangle \tag{2}$$

We will show how $\bar{T}_\delta(N_o, E)$ can be calculated.

In most biological systems, the modeling of stochastic effects is a difficult problem. We present a phenomenological approach, in which deterministic equations are reinterpreted in a birth and death framework. This technique provides a way to model stochastic effects. A second approach is outlined in the appendix.

In §2 , we rederive model B of Clark and Mangel (1977) in a more general setting. We non-dimensionalize the equations, so that the appropriate parameters become clear. The validity of the steady state assumption of Clark and Mangel can then be studied. We also discuss the (N, Q) phase plane, where N is the underlying population level and Q is the surface population level. Next, we show how to incorporate stochastic effects into the model and formulate the probabilistic questions of interest.

In §3, we construct solutions of the deterministic kinetic equations for N, Q by using a singular perturbation technique (Lin and Segel, 1973). In particular, we give a simple technique for the calculation of $T_\delta(N_o, E)$, accurate to order $1/E$. In §4, we consider stochastic effects in the steady state approximation $\dot{Q} = 0$. Exact solutions of many problems are possible. In particular, we can calculate $\bar{T}_\delta(N_o, E)$ exactly. Finally, in §5, we discuss stochastic problems in the (N, Q) phase plane. The relevant theory for the stochastic problem is given by Ludwig (1975) and Mangel (1977). We will sketch the application of those theories, but will not go into great detail. There are two appendices. In the first, we prove a theorem that generalizes the work of Clark and Mangel. In the second, we provide an alternative technique for the modeling of fluctuations.

SECTION 2

DERIVATIONS AND SCALING, STOCHASTIC MODELS

We generalize the model of Clark and Mangel, without the steady state assumption; and then non-dimensionalize. This procedure will allow us to study the validity of the steady state assumption. Next, we introduce the stochastic model and certain associated probabilistic questions.

THE AGGREGATION MODEL AND SCALING

Let $N(t)$, $Q(t)$ denote the underlying population level and surface population level, respectively, at time t. The fundamental assumption is that underlying population aggregates at the surface at a rate

$$R_a = \tilde{\alpha} N(1 - Q/\bar{Q}) \tag{3}$$

In equation (3), $\tilde{\alpha}$ is a parameter with units $(\text{time})^{-1}$; it is the association rate. $\bar{Q}$ is a constant. One might view $\bar{Q}$ as the carrying capacity of the surface level. The important point about the form of (3) is that the surface population level is limited, regardless of the value of N (Clark and Mangel, 1977). In fact, the qualitative results reported here will hold for any aggregation model in which the surface population level is limited (see appendix A).

We assume that the population has a natural growth rate $g_N(N)$. In many instances, we assume that g_N is logistic:

$$g_N(N) = rN(1 - N/\bar{N}) . \tag{4}$$

We also assume that the surface population is harvested at a rate bE , where b is a constant and E is fishing effort. We let X_o denote the average fraction of the surface level removed during one harvesting operation. The dynamical equations for surface and underlying stock evolution are:

$$\frac{dN}{dt} = g_N - \tilde{\alpha}N(1 - \frac{Q}{\bar{Q}}) \tag{5}$$

$$\frac{dQ}{dt} = \tilde{\alpha}N(1 - \frac{Q}{\bar{Q}}) - bEX_oQ . \tag{6}$$

We now show that these lead to the results of Clark and Mangel. We assume that $dQ/dt = 0$, i.e., the surface level rapidly achieves a steady state. Then

$$Q_{ss} = \frac{\tilde{\alpha}N\bar{Q}}{\bar{Q}bEX_o + \tilde{\alpha}N} \quad . \tag{7}$$

The rate at which the surface population is harvested is:

$$Y = bEX_oQ \cdot K = \frac{bEX_o \, \tilde{\alpha}N\bar{Q}}{\tilde{\alpha}N + bEX_o\bar{Q}} \tag{8}$$

Equation (8) is the result (15B) of Clark and Mangel. The steady state assumption assumes that deviations from Q_{ss} die off on a

rapid time scale. In order to calculate this time scale, we non-dimensionalize the equations.

Let

$$n = \frac{N}{\bar{N}} \qquad q = \frac{Q}{\bar{Q}} \qquad \tau = rt$$
$$\alpha = \frac{\tilde{\alpha}}{r} \qquad \beta = \frac{\bar{N}}{\bar{Q}} \qquad \bar{\lambda} = \frac{bEX_o}{r} \tag{9}$$

Then equations (5, 6) become

$$\frac{dn}{d\tau} = n(1 - n) - \alpha n(1 - q) \tag{10}$$

$$\left(\frac{1}{\alpha\beta}\right)\frac{dq}{d\tau} = n(1 - q) - \frac{\bar{\lambda}}{\beta} q \tag{11}$$

We define $\alpha\beta = 1/\varepsilon$ and $\bar{\lambda}/\beta = \lambda$ so that (11) becomes

$$\varepsilon \frac{dq}{d\tau} = n(1 - q) - \lambda q. \tag{12}$$

When $\alpha\beta = \dfrac{\tilde{\alpha}\bar{N}}{r\bar{Q}}$ is large, ε is small. For the tuna fishery, we believe that ε is small (Clark and Mangel, 1977).

When $\varepsilon = 0$, the steady state $\bar{q}$ satisfies

$$\bar{q} = \frac{n}{\lambda + n} \tag{12a}$$

Let $\hat{q}$ denote the deviation of $q(\tau)$ from $\bar{q}$: $q(\tau) = \bar{q} + \hat{q}(\tau)$.

Then,

$$\varepsilon \frac{d\hat{q}}{d\tau} = -\hat{q}(n + \lambda) \tag{13}$$

Equation (13) allows the calculation of the rate of relaxation of deviations from $\bar{q}$, (see below).

THE (n, q) PHASE PLANE AND BIFURCATION PICTURE

We now consider the phase plane described by equations (10) and (12). Steady states (or equilibria) are determined by setting the left-hand sides equal to zero. We obtain:

$$q = \frac{n}{\lambda+n} \tag{14}$$

$$0 = n(1 - n) - \alpha n\left(\frac{\lambda}{\lambda+n}\right) \tag{15}$$

The origin (0, 0) is always a steady state. The other steady states are the roots of:

$$0 = (1 - n)(\lambda + n) - \alpha\lambda$$

or (16)

$$0 = -n^2 + n(1 - \lambda) - \alpha\lambda + \lambda$$

Hence, there will be another real steady state if

$$D = (1 - \lambda)^2 - 4\lambda(\alpha - 1) > 0 \tag{17}$$

We distinguish two cases. In the first case, $\alpha < 1$. Then $D > 0$ for all values of λ . Hence, we always observe another

steady state. It is easy to show that there is only one non-negative steady state. The phase plane is sketched in figure 1. When $\alpha > 1$, a more interesting phenomenon occurs. We obtain two non-trivial steady states if

$$\alpha < 1 + \frac{(\lambda - 1)^2}{4\lambda} \tag{18}$$

The phase plane in this case is shown in figure 2. The condition $D = 0$ allows us to construct a "bifurcation" diagram in the (α, λ) plane. Such a diagram is shown in figure 3. We note that this bifurcation diagram corresponds to the "fold" catastrophe and not the "cusp" catastrophe (compare, e.g., Jones and Walters (1976)). The bifurcation value of λ is determined by $D = 0$, i.e.,

$$\alpha = 1 + \frac{(\lambda_B - 1)^2}{4\lambda_B} \tag{18a}$$

STOCHASTIC MODELS

At the present time, there is much discussion concerning the "proper" way of introducing stochastic models into biological problems (e.g., Turelli (1977) or Ludwig (1975)). Ideally, one would start with a discrete model and take appropriate limits to obtain deterministic and/or stochastic equations (Ludwig, (1975). Here, we shall take a different approach and will formally re-interpret the kinetic equations (10, 12) to obtain a stochastic model, as is done by Mangel (1977).

We start with equations (5, 6) rewritten in the form

$$\frac{dN}{dt} = \left[rN + \frac{\tilde{\alpha}NQ}{\bar{Q}}\right] - \left[\frac{rN^2}{\bar{N}} + \tilde{\alpha}N\right] \equiv b^N(N, Q) \tag{19}$$

$$\frac{dQ}{dt} = \tilde{\alpha}N - \left[\frac{\tilde{\alpha}NQ}{\bar{Q}} + bEX_oQ\right] \equiv b^Q(N, Q) \tag{20}$$

In (19, 20), we have rescaled N, Q so that they represent population level in numbers (rather than biomass). Equations (19, 20) are assumed to represent the evolution of the average value of random variables $\tilde{N}(t)$, $\tilde{Q}(t)$ that satisfy stochastic kinetic equations

$$d\tilde{N} = b^N(\tilde{N}, \tilde{Q})dt + \sqrt{A^{Nj}}\, dW_j \tag{21}$$

$$d\tilde{Q} = b^Q(\tilde{N}, \tilde{Q})dt + \sqrt{A^{Qj}}\, dW_j \tag{22}$$

In (21, 22), we use the convention of summation over repeated indices. The process $W(t)$ is a Wiener process. Although we are using an Ito equation, we shall use the Stratonovich interpretation (Wong (1971) ,(Turelli (1977)). The functions $A^{ij}(N, Q)$ are defined by,

$$A^{ij}(N, Q) = \lim_{\Delta t \to 0} \frac{1}{\Delta t} E\left\{\left(X^i(t+\Delta t) - X^i(t)\right)\left(X^j(t+\Delta t) - X^j(t)\right) \middle| X^k = X\right\} \tag{23}$$

where X^i, X^j, X^k are $\tilde{N}$ or $\tilde{Q}$. In order to calculate these variances, we reinterpret (19, 20) as follows:

$$b^N(N, Q) = b_+^N - b_-^N \tag{24}$$

$$b^Q(N, Q) = b_+^Q - b_-^Q \tag{25}$$

where

$$b_+^N = rN + \frac{\tilde{\alpha}NQ}{\bar{Q}} \qquad b_-^N = \frac{rN^2}{\bar{N}} + \tilde{\alpha}N \tag{26}$$

$$b_+^Q = \tilde{\alpha}N \qquad b_-^Q = \frac{\tilde{\alpha}NQ}{\bar{Q}} + bEX_oQ \tag{27}$$

We view b_+^N, b_+^Q as "birth rates"; b_-^N, b_-^Q as "death rates". Consider the increments $\Delta\tilde{N} = \tilde{N}(t+\Delta t) - \tilde{N}(t)$, $\Delta\tilde{Q} = \tilde{Q}(t+\Delta t) - \tilde{Q}(t)$, given that $\tilde{N}(t) = N$, $\tilde{Q}(t) = Q$, we assume that

$$\Pr\left\{\Delta\tilde{N} = 1,\ \Delta Q = 0\right\} = rN\Delta t + o(\Delta t)$$

$$\Pr\left\{\Delta\tilde{N} = 1,\ \Delta Q = -1\right\} = \frac{\tilde{\alpha}NQ}{\bar{Q}}\ \Delta t + o(\Delta t)$$

$$\Pr\left\{\Delta\tilde{N} = -1,\ \Delta Q = 0\right\} = \frac{rN^2}{\bar{N}}\ \Delta t + o(\Delta t) \tag{27a}$$

$$\Pr\left\{\Delta\tilde{N} = -1,\ \Delta Q = 1\right\} = \tilde{\alpha}N\Delta t + o(\Delta t)$$

$$\Pr\left\{\Delta\tilde{N} = 0,\ \Delta\tilde{Q} = -1\right\} = bEX_oQ\Delta t + o(\Delta t)$$

$$\Pr\left\{\text{all other transitions}\right\} = o(\Delta t)$$

We note that

$$\lim_{\Delta t \to 0} \frac{1}{\Delta t} E\{\Delta \tilde{N}\} = b^N(N, Q) \tag{28}$$

$$\lim_{\Delta t \to 0} \frac{1}{\Delta t} E\{\Delta \tilde{Q}\} = b^Q(N, Q) \tag{29}$$

Hence, the mean evolution of the stochastic equation is the deterministic evolution. We easily find

$$A = \begin{bmatrix} b_+^N(N, Q) + b_-^N(N, Q) & -\tilde{\alpha}N(1 + \frac{NQ}{\overline{Q}}) \\ -\tilde{\alpha}N(1 + \frac{NQ}{\overline{Q}}) & b_+^Q(N, Q) + b_-^Q(N, Q) \end{bmatrix} \tag{30}$$

For the dimensionless equations,

$$d\tilde{n} = b^n(\tilde{n}, \tilde{q})dt + \sqrt{a^{nj}}\, d\tilde{W}_j \tag{31}$$

$$d\tilde{q} = b^q(\tilde{n}, \tilde{q})dt + \sqrt{a^{qj}}\, d\tilde{W}_j \tag{32}$$

we find, using the same procedure, that

$$a = \begin{bmatrix} \frac{1}{\overline{N}} \{n + n^2 + \alpha n + \alpha nq\} & -\alpha n(1 + q) \\ -\alpha n(1 + q) & \frac{1}{\overline{Q}} \cdot \frac{1}{\varepsilon} \{n + q + \lambda q\} \end{bmatrix} \tag{33}$$

We now consider a number of probabilistic quantities connected with the stochastic equations. We use the notation, b^i for b^N or b^Q and a^{ij} for the elements of a. We denote by $x^1 = \tilde{N}$ or $\tilde{n}$ and $x^2 = \tilde{Q}$ or $\tilde{q}$. First consider the density for (x^1, x^2):

$$v(x^1,x^2,t)dx^1dx^2 = \Pr\{\tilde{x}^1(t) \in (x^1,x^1+dx^1),\ \tilde{x}^2(t) \in (x^2,x^2+dx^2)\} \tag{34}$$

Then v satisfies the forward equation (Ludwig, 1975):

$$v_t = \left(\frac{a^{ij}}{2}v\right)_{ij} - \left((b^i + c^i)v\right)_i \tag{35}$$

In equation (35),

$$c^i(x) = \frac{1}{4}\frac{\partial}{\partial x^j} a^{ij} \tag{36}$$

The function $c(x)$ arises in the Stratonovich interpretation of the equations (31, 32). In (35), subscripts indicate partial differentiation and repeated indices are summed. The density is subject to the normalization condition,

$$\iint v(x^1,x^2)dx^1dx^2 = 1. \tag{37}$$

Let $p(x^1, x^2, t)$ be defined by

$$p(x^1,x^2,t) = \Pr\{\tilde{x}^1(t) \le \delta \,|\, \tilde{x}^1(0) = x^1,\ \tilde{x}^2(0) = x^2\} \tag{38}$$

Then p will satisfy the backward equation (Ludwig, 1975)

$$p_t = \frac{1}{2}a^{ij}p_{ij} + (b^i + c^i)p_i \tag{39}$$

subject to boundary and initial conditions

$$p(\delta, x^2, t) = 1 \qquad \lim_{x^1 \to \infty} p(x^1, x^2, t) = 0 \tag{40}$$

$$p(x^1, x^2, 0) = \begin{cases} 0 & x^1 > \delta \\ 1 & \text{otherwise} \end{cases}$$

Finally, we consider the expected time to cross a given line

$$\begin{aligned} T(\delta; x_o^1, x_o^2) &= E\{t : \tilde{x}^1(t) \le \delta, \tilde{x}^1(s) > \delta, s < t \,|\, \tilde{x}^1(0) = \\ &\quad x_o^1, \tilde{x}^2(0) = x_o^2, \tilde{x}^1(t) \text{ eventually crosses } \delta\} \end{aligned} \tag{41}$$

Then T satisfies

$$-p(x_o^1, x_o^2) = \frac{1}{2} a^{ij} T_{ij} + (b^i + c^i) T_i \tag{42}$$

where $p(x_o^1, x_o^2)$ is the steady state solution of (38) (e.g., Gihman and Skorohod(1972)). In the case that we use the steady state (ε=O) assumption equations (36), (39), (42) simplify, as will be seen.

SECTION 3

A TWO-TIMING METHOD FOR $n, \hat{q}$

We now return to the deterministic equations (10),(12) and analyze them. In section 4, 5 we consider the stochastic equations. Equations (10),(12) represent a singular perturbation problem. It is clear that for times $\tau \gg \varepsilon$, q has achieved its steady state $\bar{q}$, so that $\hat{q} = 0$. Our goal in this section is to calculate the rate at which $\hat{q} \to 0$. We introduce an "initial layer" time scale

$$S = \frac{\tau}{\varepsilon} \tag{43}$$

Then equations (10), (12) become

$$\frac{dn}{dS} = \varepsilon\{n(1-n) - \frac{\alpha\lambda n}{\lambda+n} + \alpha n\hat{q}\} \qquad n(0) = N_o \tag{44}$$

$$\frac{d\hat{q}}{dS} = -(n+\lambda)\hat{q} \qquad \hat{q}(0) = Q_o \tag{45}$$

We seek a solution of the form

$$n(S) = n_o(S) + \varepsilon n_1(S) + \varepsilon^2 n_2(S) + \ldots \tag{46}$$

$$\hat{q}(S) = \hat{q}_o(S) + \varepsilon\hat{q}_1(S) + \varepsilon^2\hat{q}_2(S) + \ldots \tag{47}$$

After the series (46, 47), are substituted into (44, 45), terms are collected according to powers of ε . We use the expansion

$$\frac{1}{\lambda+n} = \frac{1}{\lambda+n_o}\left(1 - \frac{\varepsilon n_1}{\lambda+n_o} + \ldots\right) \tag{48}$$

The $O(1)$ terms indicate that

$$\frac{dn_o}{dS} = 0 \qquad \text{i.e.,} \quad n_o = N_o \tag{49}$$

$$\frac{d\hat{q}_o}{dS} = -(n_o + \lambda)\hat{q}_o$$

$$= -(N_o + \lambda)\hat{q}_o \tag{50}$$

Thus,

$$\hat{q}_o(S) = Q_o \exp[-(N_o + \lambda)S] \tag{51}$$

To leading order in ε, $\hat{q}(S)$ relaxes towards 0 with a relaxation time

$$\tau_R = \frac{1}{N_o+\lambda} \tag{52}$$

Corrections to the above relaxation time can be obtained by considering further terms in the series. The $O(\varepsilon)$ terms indicate that,

$$\frac{dn_1}{dS} = N_o - N_o^2 - \frac{\alpha\lambda N_o}{\lambda + N_o} + \alpha N_o \hat{q}_o \tag{53}$$

$$\frac{d\hat{q}_1}{dS} = -\hat{q}^1 (N_o + \lambda) - \hat{q}_o n_1 . \tag{54}$$

These equations do not have a simple solution.

Next we consider the "outer" equations, in the time variable τ .

We seek solutions of (10, 12) of the form

$$n(\tau) = \sum_{j=0} \varepsilon^j \bar{n}_j(\tau) \tag{55}$$

$$q(\tau) = \sum_{j=0} \varepsilon^j \bar{q}_j(\tau) \tag{56}$$

The $0(1)$ terms indicate that

$$\frac{d\bar{n}_o}{d\tau} = \bar{n}_o - \bar{n}_o^2 - \frac{\alpha\lambda\bar{n}_o}{\lambda + \bar{n}_o} + \alpha\bar{n}_o\bar{q}_o \tag{57}$$

$$0 = -\bar{q}_o(\bar{n}_o + \lambda) \tag{58}$$

Hence, we obtain the steady state result of Clark and Mangel (1977)

$$\frac{d\bar{n}_o}{d\tau} = \bar{n}_o - \bar{n}_o^2 - \frac{\alpha\lambda\bar{n}_o}{\lambda + \bar{n}_o} \tag{59}$$

In the limit that $\lambda << \bar{n}_o$, (59) becomes

$$\frac{d\bar{n}_o}{d\tau} = \bar{n}_o - \bar{n}_o^2 - \alpha\lambda. \tag{59a}$$

Equation (59a) is the "constant-yield" equation studied by Brauer and Soudack.

No simple solution for $n_o(T)$ is available in terms of elementary functions. Consequently, the usual "matching" procedures of singular perturbation theory (e.g., Lin and Segel (1977)) are not very helpful. (Simple considerations show that the matching procedure must yield $\bar{n}_o(0) = N_o$.)

We now consider equation (59) for the special case that $\alpha > 1$ and $\lambda > \lambda_B$, the bifurcation value of λ. In this case, the origin is the only steady state. Consequently, the population is driven to extinction. Let

$$T(\delta, N_o) = \min\{t : \bar{n}_o(t) \leq \delta,\ \bar{n}_o(S) > \delta\ S < t,\ \bar{n}_o(0) = N_o\} \tag{60}$$

The interpretation of $T(\delta, N_o)$ is as an "extinction time", if δ is small. We will now construct a second perturbation expansion, for large λ, in order to calculate $T(\delta, N_o)$.

Equation (59) can be inverted to give:

$$\frac{dT}{d\bar{n}_o} = \frac{\lambda + \bar{n}_o}{\bar{n}_o(1 - \bar{n}_o)(\lambda + \bar{n}_o) - \alpha\lambda\bar{n}_o} \qquad T(N_o) = 0 \tag{61}$$

We introduce $\Gamma = 1/\lambda$ as a second small parameter, so that

$$\frac{dT}{d\bar{n}_o} = \frac{1 + \Gamma\bar{n}_o}{\bar{n}_o(1 - \bar{n}_o)(1 + \Gamma\bar{n}_o) - \alpha\bar{n}_o} \tag{62}$$

We seek a solution of (62) in the form

$$T = \sum_j \Gamma^j T_j(\bar{n}_o). \tag{63}$$

The leading terms satisfy

$$\frac{dT_o}{d\bar{n}_o} = \frac{1}{\bar{n}_o(1 - \bar{n}_o) - \alpha\bar{n}_o} \qquad T_o(N_o) = 0 \tag{64}$$

$$\frac{dT_1}{d\bar{n}_o} = \frac{\bar{n}_o}{\bar{n}_o(1 - \bar{n}_o) - \alpha\bar{n}_o} - \frac{\bar{n}_o^2(1 - \bar{n}_o)}{[\bar{n}_o(1 - \bar{n}_o) - \alpha\bar{n}_o]^2} \qquad T_1(N_o)=0 \tag{65}$$

These equations can be easily solved. Thus, we find:

$$T(\delta, N_o) = \frac{1}{1-\alpha}\left[\ln\left(\frac{\delta}{N_o}\right) - \ln\left(\frac{1-\alpha-\delta}{1-\alpha-N_o}\right)\right]$$

$$+ \frac{\alpha^2}{\lambda}\left\{\frac{1}{(\alpha-1) + \delta} - \frac{1}{(\alpha-1) + N_o}\right\} + O\left(\frac{1}{\lambda^2}\right) \tag{66}$$

In summary, the result (66) was obtained by using <u>two perturbation</u> procedures. First, we used a singular perturbation procedure to calculate the relaxation time τ_R and to obtain (59). Second, a regular perturbation procedure was used to calculate $T(\delta, N_o)$.

To check the accuracy of the steady state assumption, $T(\delta, N_o)$ calculated from (66) was compared with the exact solution of (10,13), by a Runge-Kutta method. We chose $\tilde{q}(0) = 1$, $\varepsilon = 1$, $\delta = .1$. In table 1, some results of the calculation are presented. Since $\varepsilon = 1$, in principle,the use of the steady state assumption is not warranted. However, the results in table 1 indicate that the steady state assumption provides a relatively good description of the system, even for ε order 1.

SECTION 4

EXTINCTION IN A RANDOM ENVIRONMENT: STEADY STATE CASE

We now consider some of the stochastic problems presented in section 2.3, assuming that the steady state assumption ($\varepsilon = 0$) about $\hat{q}$ holds. Hence, the stochastic equations (31, 32) are replaced by,

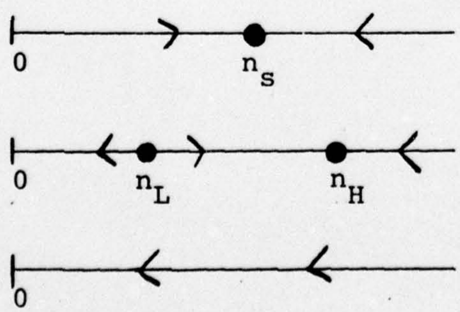
$$d\tilde{n} = \left[\tilde{n}(1 - \tilde{n}) - \frac{\alpha\lambda\tilde{n}}{\lambda+\tilde{n}}\right] dt + \sqrt{\sigma a(n)}\, dW \tag{67}$$

where $\sigma = 1/\bar{N}$ and

$$a(n) = n + n^2 + \frac{\alpha\lambda n}{\lambda+n} \tag{68}$$

When $\sigma = 0$ (i.e., $1/\bar{N} = 0$) we obtain the *deterministic kinetic* equation (59) from (67). This is in accord with intuition: as the sample size becomes larger, fluctuation effects should disappear.

The flow of the deterministic equation is sketched below (these pictures are transcriptions of the results in section 2):



$\alpha < 1$, all λ

$\alpha > 1$, $\lambda < \lambda_B$

$\alpha > 1$, $\lambda > \lambda_B$

In order to simplify calculations, we shall approximate $\alpha(n)$ by n. Since the stochastic effects are most interesting when n is small, this approximation (which greatly simplifies calculations) seems reasonable.

THE DENSITY $v(n, t)$

The forward equation for $v(n, t)$ (35) becomes,

$$v_t = \frac{\sigma}{2} (nv)_{nn} - \left[\{n(1-n) - \frac{\alpha\lambda n}{\lambda+n} + \frac{\sigma}{4}\}v\right]_n \tag{68}$$

The first question we wish to consider is the calculation of the stationary distribution, $v(n)$. If $v_t = 0$, (68) becomes an ordinary differential equation that can be integrated to yield,

$$v(n) = c \exp\left[\frac{2}{\sigma}\left\{n - \frac{n^2}{2} - \alpha\lambda \ln\left(\frac{1+n}{\lambda}\right) - \frac{\sigma^2}{2} \ln n\right\}\right] \tag{69}$$

$$= c \exp\left[\frac{-2}{\sigma} \phi(n)\right] \tag{69a}$$

The constant c is determined by normalization:

$$c = \left[\int_0^\infty \exp\left[\frac{-2}{\sigma} \phi(n)\right] dn\right]^{-1} \tag{70}$$

The probability of eventually finding the population at a level less than δ is,

$$P_\delta = \int_0^\delta v(n)dn. \tag{71}$$

Natural questions concern the location of concentration points of $v(n)$ and the behavior of $v(n)$ for λ large. The density $v(n)$

will be concentrated near the minima of the function $\phi(n)$. It is easy to show that these minima correspond to the steady states of the deterministic kinetic equation.

When λ is large, we expand $\ln(1 + n/\lambda)$ in its Taylor series and obtain,

$$v(n) = c \exp\left[\frac{2}{\sigma}\left\{n - \frac{n^2}{2} - \alpha\lambda\left(\frac{n}{\lambda} - \frac{n^2}{2\lambda^2}\right) + O\left(\frac{1}{\lambda^3}\right) - \frac{\sigma^2}{2}\ln n\right\}\right] \tag{72}$$

Thus, for small σ and large λ:

$$v(n) \sim c \exp\left[\frac{2}{\sigma}\left\{n(1-\alpha) - \frac{n^2}{2}\left(1 - \frac{\alpha}{\lambda}\right)\right\}\right] \tag{73}$$

In this case, the extremum of ϕ occurs at

$$n^* = \frac{1-\alpha}{1-\frac{\alpha}{\lambda}} \tag{74}$$

The result (76) indicates the following. If $\alpha < 1$, then $n^* > 0$ always, so that the density is concentrated near n^*. When $\alpha > 1$, $n^* > 0$ if λ is small enough. In particular, $n^* > 0$ if

$$1 - \frac{\alpha}{\lambda} < 0 \qquad \text{i.e.,} \quad \lambda < \alpha \tag{76}$$

Equation (76) can be viewed as a stochastic bifurcation result. We note that, for $\alpha > 1$, n^* corresponds to a minimum of $v(n)$.

MEAN TIME TO CROSS $n = \delta$

We now turn to the calculation of the mean time to cross the level $n = \delta$, conditioned on $n(0) = N_o$. This function $\overline{T}(\delta, N_o)$ satisfies

$$\frac{\sigma n}{2} \overline{T}_{nn} + \left[n(1-n) - \frac{\alpha\lambda n}{\lambda+n} + \frac{\sigma}{4}\right] \overline{T}_n = -p(n) \tag{77}$$

In (77), $p(n) = \Pr\{\tilde{n}(t) \text{ eventually crosses } \delta | \tilde{n}(0) = n\}$.
The function $\overline{T}$ satisfies the boundary conditions:

$$\overline{T}(\delta, \delta) = 0 \qquad \lim_{n\to\infty} T_n(\delta, n) = 0 \tag{78}$$

The function $p(n)$ satisfies:

$$\frac{\sigma n}{2} p_{nn} + \left[n(1-n) - \frac{\alpha\lambda n}{\lambda+n} + \frac{\sigma}{4}\right] p_n = 0 \tag{79}$$

subject to

$$p(\delta) = 1 \qquad \lim_{n\to\infty} \;\&\; p(n) \to 0 \tag{80}$$

Both the functions $p(n)$ and $T(\delta, n)$ can be calculated explicitly by two integrations:

$$p(n) = \frac{\int_n^\infty \exp\left[-\frac{2}{\sigma}\left\{n' - \frac{(n')^2}{2} - \alpha\lambda \ln(1+\frac{n'}{\lambda}) - \frac{\sigma}{2}\ln n'\right\}\right] dn'}{\int_\delta^\infty \exp\left[-\frac{2}{\sigma}\left\{n' - \frac{(n')^2}{2} - \alpha\lambda \ln(1+\frac{n'}{\lambda}) - \frac{\sigma}{2}\ln(n')\right\}\right] dn'} \tag{81}$$

In many cases of interest, $p(n) \approx 1$ for almost all values of n. The solution of the problem posed by (77,78) is,

$$T(n) = \frac{2}{\sigma}\int_0^n \exp\left[\frac{-2}{\sigma}\left\{S - \frac{S^2}{2} - \alpha\lambda \,\ell n(1+\frac{S}{\lambda}) - \frac{\sigma}{2}\,\ell n\, S\right\}\right] x$$

$$\int_S^\infty \exp\left[\frac{2}{\sigma}\left\{y - \frac{y^2}{2} - \alpha\lambda \,\ell n\,(1+\frac{y}{\lambda}) - \frac{\sigma}{\lambda 2}\,\ell n\, y\right\}\right] p(y)\,dy\,dS \qquad (82)$$

The behavior of $p(n)$, $T(\delta, n)$ is sketched in figure 4, for a number of cases. Equations (81, 82) allow the explicit calculation of the mean time to extinction in the stochastic case.

SECTION 5

EXTINCTION IN A RANDOM ENVIRONMENT, WITHOUT THE STEADY STATE ASSUMPTION

In two dimensions the $[(n,\hat{q})$ or (n,q) phase space$]$ no exact solutions of the stochastic problems are possible. If the intensity of the noise is small (i.e., $1/\bar{N}$, $1/\bar{Q}$ large), then approximate theories are available (Ludwig (1975), Mangel (1977)). In this section, we will sketch how those theories apply to the aggregation problem. We wish to calculate: 1) the probability that $\tilde{n}(t)$ ever crosses the line $n = \delta$, conditioned on initial value of n, and 2) the mean time to cross the line $n = \delta$. We differentiate two cases, according to the values of α.

$\alpha < 1$; THE RAY METHOD (LUDWIG,1975)

When $\alpha < 1$ (figure 1), the non-trivial steady state is always stable. Hence, we are interested in the exit from the domain $n > \delta$. The density of (n,q), $v(\tau,n,q)$, satisfies the forward equation

$$v_\tau = \frac{\sigma}{2}(a^{ij}v)_{ij} - ((b^i + \sigma c^i)v)_i \tag{83}$$

with $a(n,q)$, $c(n,q)$ given by (33), (36) respectively and $b^1 = \frac{dn}{d\tau}$, $b^2 = \frac{dq}{d\tau}$ in (10,12). We assume that $\varepsilon = 1$. Ludwig (1975) has shown that the ray method (Cohen and Lewis, 1967) applies here. A solution of (83) of the form,

$$v(\tau,n,q) = \exp\left[\frac{-\phi(\tau,n,q)}{\sigma}\right] \sum_{j=0}^{\infty} z_j\sigma^j \tag{84}$$

is sought.

After derivatives are evaluated, terms are collected according to powers of σ. The leading term vanishes if

$$b^i \phi_i + \frac{a^{ij}}{2} \phi_i \phi_j = 0 \tag{85}$$

To first order, Z_o satisfies an ordinary differential equation on the characteristics of (85).
Equation (85) can be solved by the method of characteristics, once initial data are given. Ludwig has shown how this may be accomplished. The characteristics of the system (85) are called rays.

Suppose that $v \sim 0$ on the boundary and that we assume for v,

$$v(\tau,n,q) = \sum_{k=0} e^{-\lambda_k \tau} \bar{v}(n,q) \tag{86}$$

Then the expected time to hit the boundary is asymptotic to $1/\lambda_o$ (Ludwig, 1975). We are led to the eigenvalue problem

$$-\lambda_o = \frac{\sigma}{2} (a^{ij}v)_{ij} - ((b^i + \sigma c^i)v)_i \tag{87}$$

Ludwig has shown how Miller's method (Miller, 1962) may be generalized to calculate λ_o. Thus, in principle the problem is completely solved. Further details and calculations are in (Ludwig, 1975).

$\alpha \geq 1$: THE GENERALIZED RAY METHOD (MANGEL, 1977)

When $\alpha \geq 1$, there may be two non-zero steady states $(\lambda < \lambda_B)$, one degenerate steady state $(\lambda = \lambda_B)$, or only the trivial

steady state $(\lambda > \lambda_B)$ (figure 2). The ray method will break down in this case, but a generalization of the ray method does work (Mangel, 1977). Here we sketch the technique. The details can be found elsewhere. We consider $\bar{T}(\delta;\ n,q)$, which satisfies

$$-1 = \frac{\sigma}{2} a^{ij} T_{ij} + b^i T_i + c^i T_i \tag{88}$$

Asymptotic analysis of a one dimensional problem (for σ small) indicates that a formal solution of (88) is

$$\begin{aligned}\bar{T} &= g(x) B(\psi/\sigma^{1/3},\ \alpha/\sigma^{2/3},\ 1/\sigma^{1/3},\ \eta) \\ &\quad + \varepsilon^{2/3} h(x) B'(\psi/\sigma^{1/3},\ \alpha/\sigma^{2/3},\ 1/\sigma^{1/3},\ \eta) \\ &\quad + \varepsilon k(x)\end{aligned} \tag{89}$$

In (89), $B(Z,\alpha,\xi_1,\xi_2)$ satisfies the differential equation

$$\frac{d^2B}{dZ^2} = -(Z^2 - \alpha)\frac{dB}{dZ} - \xi_1 + \xi_2 Z \qquad Z_o \le Z \tag{90}$$

The functions, $g(x)$, $h(x)$, and $k(x)$ should also be expanded in asymptotic series of the form,

$$g(x) = \sum \varepsilon^n g^n(x) \qquad k(x) = \sum \varepsilon^n k^n(x) \qquad h(x) = \sum \varepsilon^n h^n(x) \tag{91}$$

where the superscript n is an index on g^n, h^n, and k^n. After derivatives are evaluated, and substituted into (88) (using equation (90) to eliminate B'' and B''') terms are collected according to powers of ε. The leading coefficients vanish if

$$O(\gamma^{-2/3}B): \quad b^i\psi^i - \frac{a^{ij}}{2}\psi_i\psi_j(\psi^2 - \alpha) = 0 \tag{92}$$

$$O(\gamma^o B): \quad b^i g_i = 0 \tag{93}$$

$$O(\gamma^o): \quad b^i k_i + \frac{a^{ij}}{2} g\psi_i\psi_j(-1 + \psi\eta) = -1 \tag{94}$$

Equation (92) is a generalized Hamilton-Jacobi equation. It can be solved by the method of characteristics. The parameter α is determined by requiring $\psi^2 = \alpha$ at the points where $b(x)$ vanishes. Namely, at the steady states P_0, P_1, $\psi^2 = \alpha$. The value of α must be determined by a numerical iterative procedure (Mangel, 1977). At $\lambda = \lambda_B$, so that P_0 and P_1 coalesce , the value of $\alpha = 0$. Equation (93) indicates that g is a constant. It's value is determined as follows. At P_0, P_1, equation (94) becomes

$$g\frac{a^{ij}}{2}\psi_i\psi_j(-1 + \psi\eta)\Big|_{P_k} = -1 \tag{95}$$

For $k = 0,1$, we obtain two equations for g and η . When $\lambda = \lambda_B$, it is possible to show that $\eta = 0$ and (95) provides one equation for g. (Mangel, 1977).

We give data $k = 0$ on $n = \delta$. Then (94) can be solved by the method of characteristics. We let $\psi = \psi_o$ on $n = \delta$, set $\psi_o = Z_o$ in (90) and $B(Z_o) = B'(Z_o) = 0$. Then $\overline{T} = 0$ on $n = \delta$. This construction will yield values for T which are $O(\sigma^{2/3})$ different from the true values. Further details can be found in Mangel (1977).

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ACKNOWLEDGEMENTS

The initial phase of this work was supported by contract number 03-6-208-35341, from the National Marine Fisheries Service.

I thank Professors C.W. Clark and D. Ludwig for helpful discussions and C.W. Clark for his comments on a previous draft of the manuscript.

APPENDIX A

THE GENERAL AGGREGATION MODEL

In this appendix, we prove a theorem that applies to the general set of aggregation equations

$$\dot{N} = g_N - \alpha f(N, Q) \tag{A-1}$$

$$\dot{Q} = \alpha f(N, Q) - \lambda Q \tag{A-2}$$

with N, Q defined as in the body of the paper.

Let $Q^*(N, \alpha, \lambda)$ be the solution of

$$\alpha f(N, Q) = \lambda Q \tag{A-3}$$

such that the following hypotheses are satisfied:

a.) $\lim_{N\to\infty} Q^*(N, \alpha, \lambda) = c_o < \infty$

b.) $\lim_{N\to\infty} \alpha f(N, Q^*(N, \alpha, \lambda) = c_1(\alpha, \lambda) < \infty$ for all α, λ

c.) $\lim_{\lambda\to\infty} \alpha f(N, Q^*(N, \alpha, \lambda)) = c_2(\alpha, N) < \infty$ for all α, N

Then there exist values α^*, λ^* such that the tuna steady state level exhibits a bifurcation. Namely, for $\alpha > \alpha^*$ and $\lambda < \lambda^*$

there are three steady state solutions, $N(\alpha, \lambda)$ of (A-1, A-2). The origin is a stable steady state. There are two other non-trivial steady states $N_S(\alpha, \lambda)$, $N_u(\alpha, \lambda)$ which are stable and unstable, respectively. When $\lambda = \lambda^*$, N_S and N_u coalesce and annihilate each other for $\lambda > \lambda^*$.

PROOF

First, we note that conditions a, b insure a finite surface population, for all underlying population levels.

The steady state underlying level is determined by solving

$$g_N(N) = \alpha f(N, Q^*(N, \alpha, \lambda)) \tag{A-4}$$

We determine α^* by solving for α the equation:

$$g_N'(0) = \alpha^* \frac{\partial}{\partial N} f(N, Q^*(N, \alpha, \lambda))\Big|_{N=0} \tag{A-5}$$

$$= \alpha^* \left\{ f_N(0, Q^*(0, \alpha^*, \lambda)) + f_Q(0, Q^*(0, \alpha^*, \lambda)) \frac{\partial Q^*}{\partial N}(0, \alpha^*, \lambda) \right\} \tag{A-6}$$

We determine $\lambda^*(\alpha)$ as follows. For any fixed α, $\alpha > \alpha^*$ consider the function

$$Y(N, \lambda) = \alpha f(N, Q^*(N, \lambda, \alpha)) - g_N(N) \tag{A-7}$$

We choose λ^* by requiring that

$$Y(N, \lambda^*) = 0 \tag{A-8}$$

has two solutions: $N = 0$ and $N = N^*$, where N^* is determined by

$$\frac{\partial}{\partial N} Y(N, \lambda^*) \Big|_{N^*} = 0 \quad . \tag{A-9}$$

Then for fixed α, $\alpha > \alpha^*$, as λ increases through λ^*, we observe a bifurcation (figure 5).

APPENDIX B

A KINETIC MODEL FOR FLUCTUATIONS

Clark and Mangel considered a kinetic model that yields the same behavior as equations (11, 12). This model provides a natural way to treat fluctuations. We let $T(t)$ be the number of "core" schools in the ocean and consider the kinetic scheme.

$$\begin{aligned} T + K &\underset{\beta_1}{\overset{\alpha_1}{\rightleftharpoons}} C_1 \\ T + C_1 &\underset{\beta_2}{\overset{\alpha_2}{\rightleftharpoons}} C_2 \\ C_1 &\xrightarrow{bEX_o} \text{harvest} + K \\ C_2 &\xrightarrow{bEX_o} \text{harvest} + K \end{aligned} \tag{B-1}$$

where C_1, C_2 are, respectively, surface complexes with 1 and 2 core schools. The kinetic equations for the scheme (B-1), derived by a "law of mass action" approach, are:

$$\frac{dT}{dt} = g_T - \alpha_1 TK - \alpha_2 TC_1 + \beta_1 C_1 + \beta_2 C_2 \tag{B-2}$$

$$\frac{dK}{dt} = g_K - \alpha_1 TK + \beta_1 C_1 + bEX_o(C_1 + C_2) \tag{B-3}$$

$$\frac{dC_1}{dt} = \alpha_1 KT - \beta_1 C_1 + \beta_2 C_2 - \alpha_2 C_1 T - bEX_o C_1 \tag{B-4}$$

$$\frac{dC_2}{dt} = \alpha_2 C_1 T - \beta_2 C_2 - bEX_o C_1 \tag{B-5}$$

The analysis of (B.2-B.5) yields results analogous to (10-12); if we set $\beta_1 = \beta_2 = 0$ (Clark and Mangel, Appendix B).

For the purpose of stochastic modeling, however, the scheme (B-1) has a number of advantages. In particular, no re-interpretation of the kinetic equation is needed, since the elementary events (B-1) are clearly a birth and death process. Consider a time increment $t \to t + \Delta t$, with the values of $T(t)$, $C_1(t)$, $C_2(t)$ and $K(t)$ known. Then in the increment Δt, we assume that the following transition probabilities exist:

$$\Pr\{\Delta T = 1,\ \Delta K = 1,\ \Delta C_1 = -1,\ \Delta C_2 = 0\} = \beta_1 C_1 \Delta t + o(\Delta t) \tag{B-6}$$

$$\Pr\{\Delta T = -1,\ \Delta K = -1,\ \Delta C_1 = 1,\ \Delta C_2 = 0\} = \alpha_1 TK \Delta t + o(\Delta t) \tag{B-7}$$

$$\Pr\{\Delta T = -1,\ \Delta K = 0,\ \Delta C_1 = -1,\ \Delta C_2 = 1\} = \alpha_2 TC_1 \Delta t + o(\Delta t) \tag{B-8}$$

$$\Pr\{\Delta T = 1,\ \Delta K = 0,\ \Delta C_1 = 1,\ \Delta C_2 = -1\} = \beta_2 C_2 \Delta t + o(\Delta t) \tag{B-9}$$

$$\Pr\{\Delta T = 0,\ \Delta K = 0,\ \Delta C_1 = -1,\ \Delta C_2 = 0\} = bEX_o C_1 \Delta t + o(\Delta t) \tag{B-10}$$

$$\Pr\{\Delta T = 0,\ \Delta K = 0,\ \Delta C_1 = 0,\ \Delta C_2 = -1\} = bEX_o C_2 \Delta t + o(\Delta t) \tag{B-11}$$

$$\Pr\{\text{all other transitions}\} = o(\Delta t), \tag{B-12}$$

where $\Delta T = T(t + \Delta t) - T(t)$, etc.

If we use a quasi-steady state approach, we replace C_1, C_2, and K by the steady state values (Clark and Mangel(1977)):

$$K = K_{eq} \tag{B-13}$$

$$C_2 = \frac{\alpha_2 C_1 T}{\beta_2 + bEX_o} \tag{B-14}$$

$$C_1 = \frac{\alpha_1 TK}{\beta_1 + \alpha_2 T + bEX_o - \left\{\dfrac{\alpha_2\beta_2 T}{\beta_2 + bEX_o}\right\}} \tag{B-15}$$

Then the transition probabilities are functions of $T(t)$ only.

We obtain

$$\Pr\{\Delta T = 1\} = \Delta t\{g_T + \beta_1 C_1 + \beta_2 C_2\} + o(\Delta t) \tag{B-16}$$

$$\equiv \lambda(T)\Delta t + o(\Delta t) \tag{B-17}$$

$$\Pr\{\Delta T = -1\} = \Delta t\{\alpha_1 KT + \alpha_2 C_1 T\} \tag{B-18}$$

$$\equiv \mu(T)\Delta t + o(\Delta t)$$

with C_1, C_2, and K given by (B.13-15). It is easy to show that

$$\frac{dT}{dt} = \lim_{\Delta t \to 0} \frac{1}{\Delta t} E\{\Delta T\} = \lambda(T) - \mu(T) \tag{B-19}$$

is the same as the law of mass action result. We can, however, immediately calculate the incremental variance needed for the diffusion approximation:

$$a(T) = \lim_{\Delta t \to 0} \frac{1}{\Delta t} E\{(\Delta T)^2\} \tag{B-20}$$

$$= \lambda(T) + \mu(T) \tag{B-21}$$

TABLE 1

α	N_o	$1/\lambda$	$T(\delta, N_o)$ Steady State	Exact	% Diff
10.05	1.0	.1	.234	.225	4.9
		.2	.244	.253	3.5
		.4	.266	.271	1.8
	.6	.1	.186	.199	6.5
		.2	.192	.204	5.8
		.4	.203	.213	4.7
	.2	.1	.074	.078	5.1
		.2	.076	.079	3.8
		.4	.078	.081	3.7
7.05	1.0	.1	.343	.373	8.0
		.2	.358	.386	5.4
		.4	.387	.410	5.6
	.6	.1	.274	.292	6.2
		.2	.282	.300	6.0
		.4	.300	.316	8.1
	.2	.1	.110	.114	3.8
		.2	.112	.116	3.4
		.4	.116	.119	2.5

α	N_o	$1/\lambda$	$T(\delta, N_o)$ Steady State	Exact	% Diff
4.05	1.0	.1	.644	.701	8.1
		.2	.673	.726	7.3
		.4	.730	.773	5.6
	.6	.1	.522	.577	6.3
		.2	.540	.573	5.8
		.4	.575	.605	5.0
	.2	.1	.213	.221	3.6
		.2	.217	.225	3.6
		.4	.225	.233	3.4
1.05	1.0	.1	6.53	7.74	15.6
		.2	7.13	8.32	14.3
		.4	8.33	9.47	12.0
	.6	.1	5.97	7.05	15.3
		.2	6.51	7.59	14.2
		.4	7.51	8.66	13.3
	.2	.1	3.37	3.94	14.4
		.2	3.65	4.25	14.1
		.4	4.21	4.91	14.2

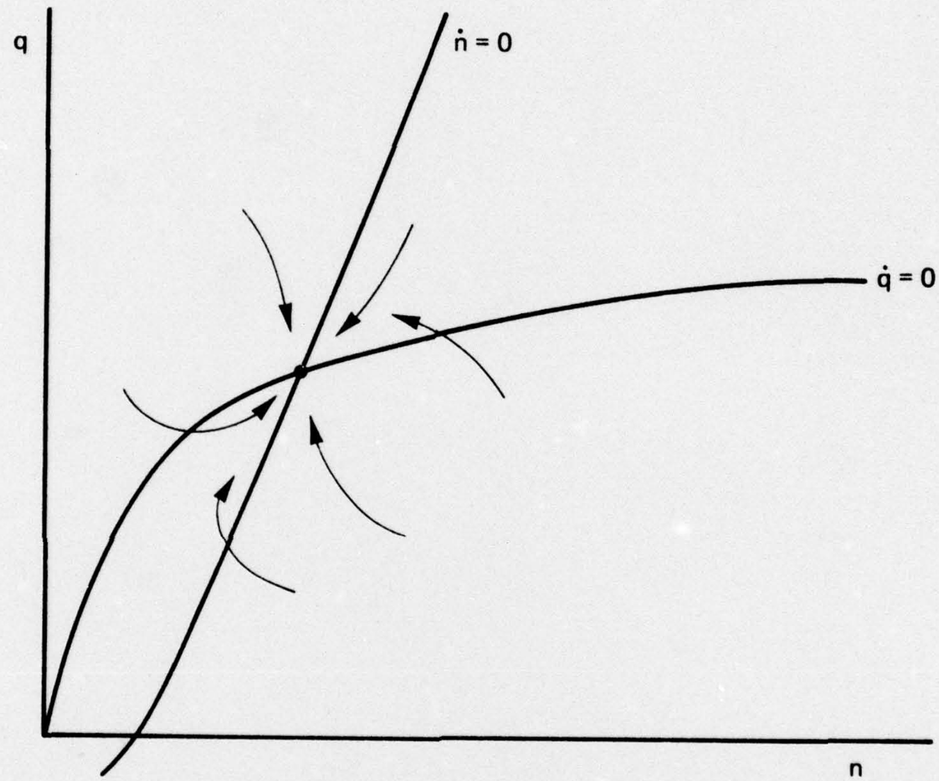

FIG. 1: The (n,q) phase plane for the case $\alpha<1$. There is a unique, stable steady state.

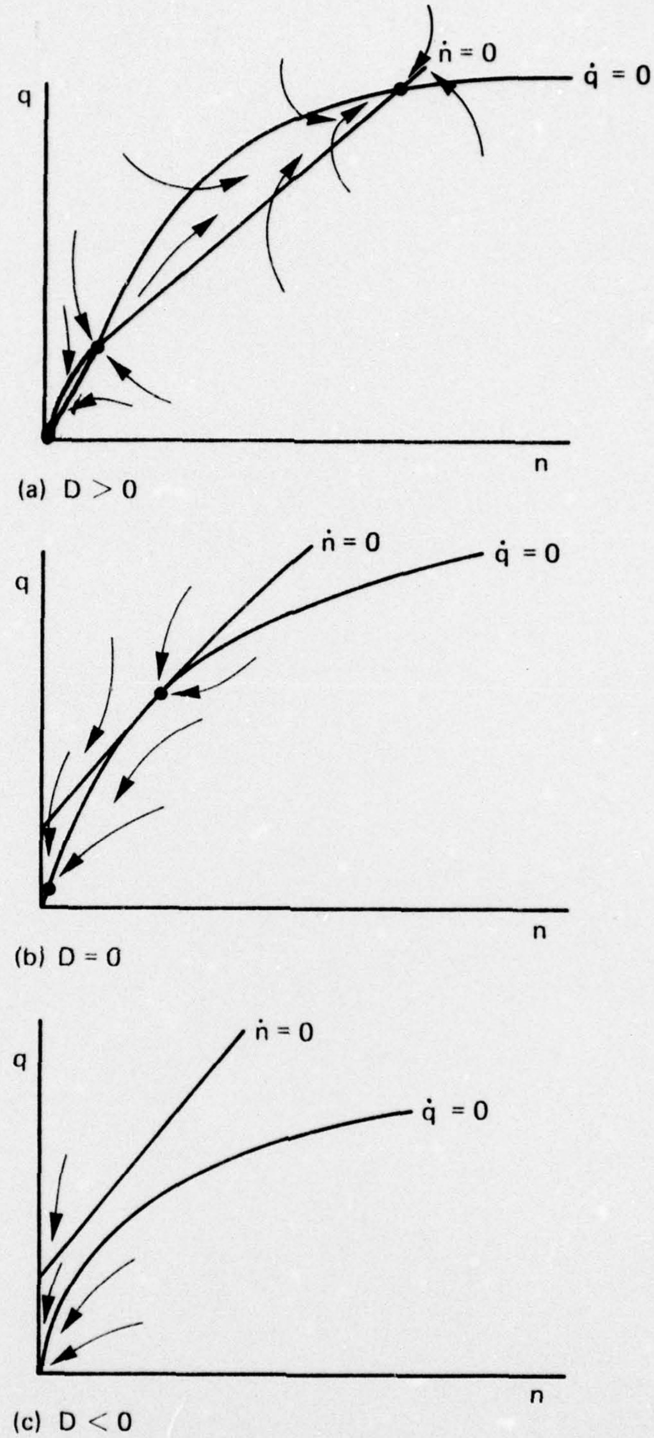

FIG. 2: The (n,q) phase plane for the case $\alpha>1$. In this case, the deterministic system is of the marginal type (Mangel, 1977). a) For $D>0$ ($\lambda<\lambda_B$) P_o is unstable. (b When $D = 0$ ($\lambda = \lambda_B$) P_o and P_1 coalesce to form a state of marginal stability. c) For $D<0$ ($\lambda>\lambda_B$) P_o and P_1 have annihilated each other. The only steady state is the origin; it is stable. The $\dot{n} = 0$ is really more parabolic than shown.

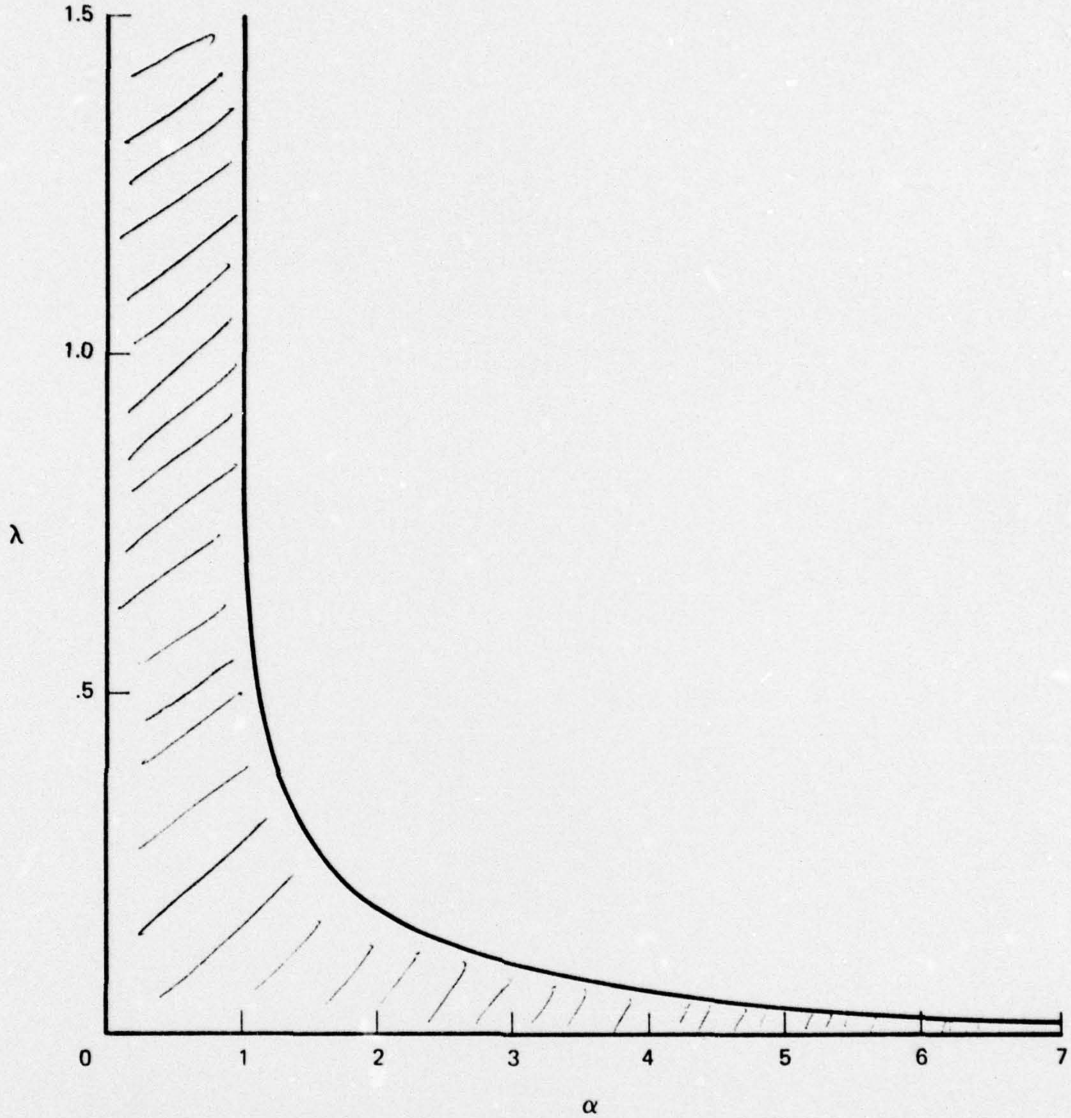

FIG. 3: The (α, λ) bifurcation picture. For points in the hatched region, there is always a nontrivial, stable steady state.

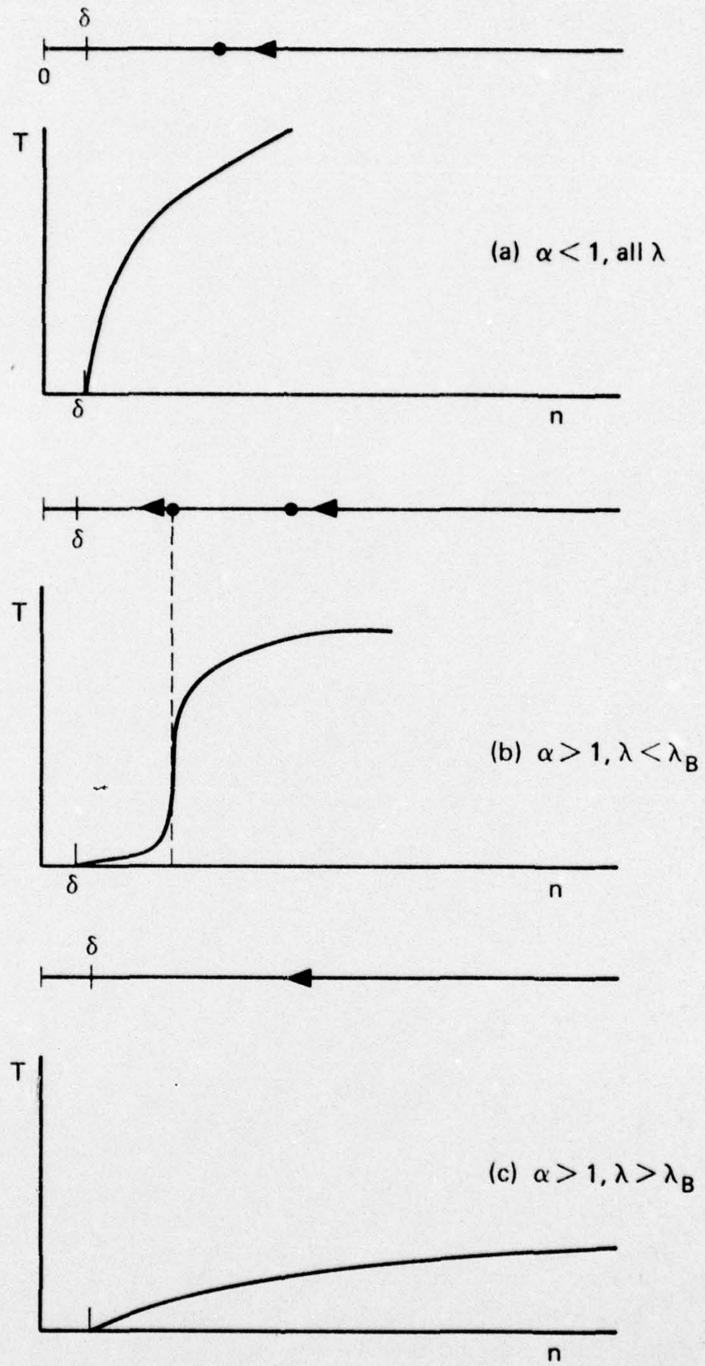

FIG. 4: The mean time to cross $n = \delta$ as a function of initial position, for the values of α ($\alpha<1, \alpha>1$) and λ ($\lambda>\lambda_B$ or $\lambda<\lambda_B$).

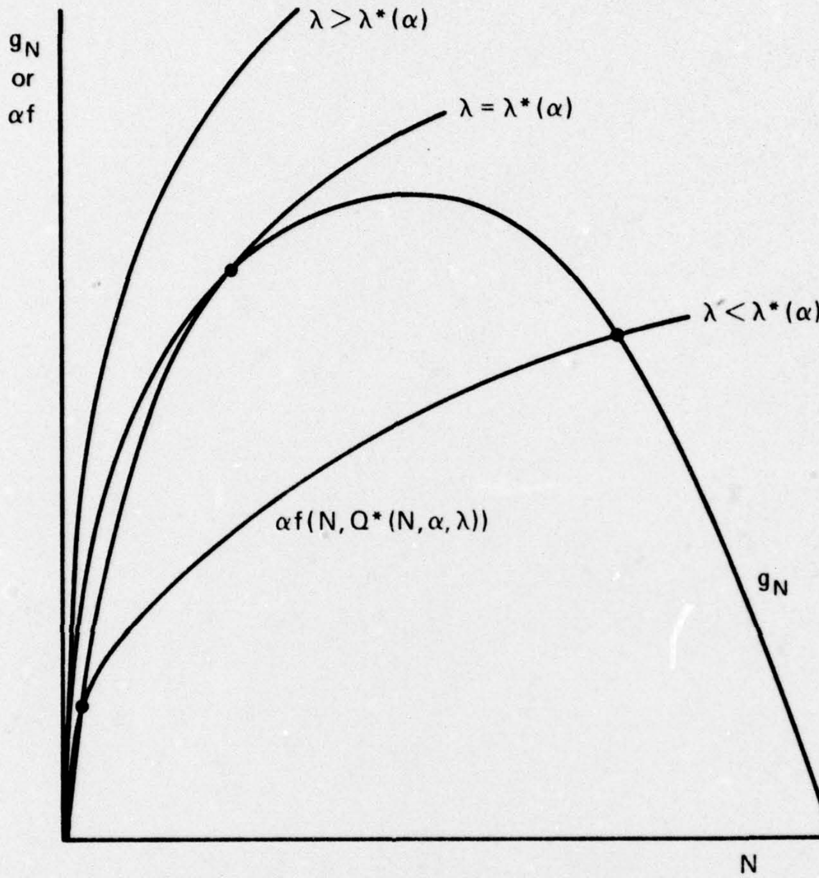

FIG. 5: Illustration of the calculation of bifurcation values α^* and λ^*.

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